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Analysis of the Probability of Multiple Taxa in a Combined Sample of Swartkrans and Kromdraai Dental Material

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ABSTRACT It has been argued (Grine, [1988] *Evolutionary History of the "Robust" Australopithecines* [New York. Aldine de Gruyter], pp. 223–243) that the australopithecine material from Swartkrans and Kromdraai represents distinct species. In an attempt to test the validity of separate taxa at Swartkrans and Kromdraai, Cope's (Cope [1989] *Systematic Variation in Cercopithecus Dental Samples* [Austin: University of Texas]) method of analysis was adapted and utilized. This procedure includes an analysis of the coefficients of variation (CVs) of the individual posterior teeth (buccal-lingual breadth) of a combined fossil sample compared with the CVs of several known single taxon reference groups. The Cope and Lacy (Cope and Lacy [1992] Am. J. Phys. Anthropol. *89*:359–378) simulation technique was also employed in the analysis. Based on these analyses, there is no justification for a taxonomic separation between the australopithecine material from Swartkrans and Kromdraai. Therefore, the assertion that the Swartkrans and Kromdraai material represent two distinct species is not indicated by the available dental metric evidence. © 1996 Wiley-Liss, Inc.

The number of australopithecine species represented by the fossil material from Swartkrans and Kromdraai continues to be a point of contention. While Macho and Thackery (1992) place this australopithecine material into the same species (*A. robustus*) for their analysis, there are other researchers (e.g., Grine, 1988) who separate the material from the two sites into different species. Grine bases his species-level distinctions on a morphological comparison of the limited deciduous dentition from those two sites (Grine, 1985, 1988). The use of deciduous dentition may relate to the fact that attempts to define morphological distinctions based on adult dental specimens are complicated by the extreme degrees of tooth wear, particularly to the M1s and M2s. From my evaluation of the relevant dental casts from Swartkrans and Kromdraai at Stony Brook, morphological variation present in these specimens appears to be more the result of differing levels of wear than of species-specific distinctions. In fact, I find no morphological evidence which would indicate clear species differences between the two samples. Grine's (1985, 1988) argument for distinctions of separate species is not convincing since it is based on small samples sizes of the deciduous teeth and an absence of any distinguishing features in the adult's teeth.

The purpose of this study is to determine whether a metrical analysis provides sufficient justification to place the material from Swartkrans and Kromdraai into separate species. If two populations have been de-

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scribed as distinct species, this distinction is testable by methods which have been used to analyze the presence of a single taxon or multiple taxa in other dental assemblages. In this case, a metrical analysis comparing the coefficients of variation (CVs) of the combined Swartkrans/Kromdaai dental material with known single taxon reference groups and with simulated single taxon populations was undertaken.

MATERIALS AND METHODS

The methodology used in this study was designed to test the hypothesis that the combined Swartkrans/Kromdraai material is drawn from a single species. For this test, a metrical comparison of combined sample (Swartkrans and Kromdraai) coefficients of variation (CVs) of maxillary and mandibular posterior teeth with the CVs of several known single taxon reference groups was undertaken. These reference groups include modern *Homo sapiens, Gorilla gorilla, Pan troglodytes*, and fossil hominids. The coefficient of variation is a statistic which enables the investigator to compare samples having different means in order to determine whether the samples differ in their degree of variability (Sokal and Rohlf, 1981). Employment of the coefficient of variation in this analysis follows from the work of Cope (1989, 1993) who, utilizing metrical data from three closely related *Cercopithecus* species, attempted to determine if there were a measure which could indicate the presence of multiple taxa in a sample.

Methodological background

The primary component of fossil assemblages is teeth. Therefore, a statistical method which can distinguish the presence of single or multiple taxa on the basis of dental characteristics is vital. Cope (1989, 1993) chose the genus *Cercopithecus* because of the difficulty in distinguishing among the many sympatric species on the basis of morphology alone. He further stated that with known *Cercopithecus* taxa differences in the central tendency of various dental traits can be noted. However, because these traits do appear at low frequencies in the other sympatric species, distinguishing species in a fossil sample on the basis of those traits alone is unlikely. Due to these factors, a metrical analysis comparing the fossil sample to reference groups is generally undertaken (Cope and Lacy, 1992).

Using dental samples of various sizes and known-species composition, Cope analyzed the three commonly used statistical methods for indicating multiple taxa: the coefficient of variation, the range as a percentage of mean, and the maximum/minimum Index. He concluded that the coefficient of variation was the most robust and least biased by sample size (Cope, 1989). This results in accord with previous research which showed that, in general, the more occlusally complex cheek teeth of primates have low variability (CVs within a narrow range) which "makes them uniquely important . . . for distinguishing closely related species in the fossil record" (Gingerich and Schoeninger, 1979).

Although Cope (1989) argued that the CVs of the lengths of posterior teeth are most useful in indicating multiple *Cercopithecus* taxa, mesial-distal length is not a precise measurement in fossil hominid material. As Robinson (1956) argued, the molars in many australopithecines are crowded by interproximal wear. Wolpoff (1971a) further notes that interproximal wear occurs at a high frequency in the other primates, particularly in chimpanzees. Since interproximal wear reduces the original length, the buccal-length breadth, which is not modified by interproximal wear, is a more accurate measurement for fossil hominids (Kieser, 1990). Cope and Lacy (1992) note that for taxa other than *Cercopithecus* the buccal-lingual breadths may be useful. For this analysis CVs of buccal-lingual breadth are used exclusively.

Cope's (1989, 1993) method for utilizing the coefficient of variation to determine the presence of multiple taxa in a fossil sample stipulates that if the CVs of the fossil sample are at or below the maximum CVs for the reference groups (chosen for their presumed close relationship to the fossil sample), then the null hypothesis of one species cannot be rejected. If several fossil sample CVs exceed the maximum of the reference groups, then it is unlikely that a single species is being sampled, if geographical variation is not a factor.

A somewhat similar approach was undertaken by Wolpoff (1978), who utilized both the coefficient of variation and the range as a percentage of the mean of the areas on anterior and posterior teeth. He then compared fossil hominid samples to pongid populations (*Gorilla* and *Pan*) and a grand average of nine modern human populations from which CVs were derived. The fossil hominid specimens were divided into four groups (South African gracile and robust forms and East African gracile and robust forms) which were compared separately and in various combinations with the reference groups.

The results of Wolpoff's analysis using CVs of dental areas were equivocal. The various fossil samples and combinations were generally more variable in each tooth than were the pongid groups but only somewhat more variable than the modern human averages. However, the fossil samples were clearly less variable than a combined pongid sample (Wolpoff, 1978). The equivocal nature of Wolpoff's analysis was possibly the result of using CVs of tooth areas rather than buccal-lingual dimensions. Since the mesiodistal dimension is affected by wear, this would adversely affect the tooth area. Also, the inclusion of the anterior dentition, with the extremely small sample sizes of incisors in the fossil material, and the probable sexually dimorphic nature of the canines in the fossil hominids, may have obscured a reliable quantification of the degree of variability in the fossil samples.

Materials

In this analysis, the fossil sample used is comprised of all known permanent maxillary and mandibular posterior australopithecine teeth for both Kromdraai and Swartkrans. (Antimeres were excluded from the Swartkrans sample by analyzing the buccal-lingual dimension and the degree of wear on the Swartkrans teeth.) The material found prior to 1979 was measured by Wolpoff (personal communication), and the new material is described by Grine (1989). Only posterior teeth were used in this analysis due to the small number of incisors and attempts to limit the effect of canine dimorphism. Data for the combined Swartkrans/Kromdaai sample are listed in Table 1.

The modern human CVs were obtained from the combined-sex samples of 11 different populations (Frayer, personal, communication; Kieser, 1990; Wolpoff, personal, communication). Only human populations with a sample size per tooth of greater than 20 were used (see Table 2). CVs for pongids were obtained from the combined-sex sample dental CVs of Mahler (1973). Finally, data used for the reference groups of fossil hominids (Afar/Laetoli and Sterkfontein/Makapansgat) were obtained from Wolpoff (personal, communication).

Since *Homo sapiens* is a polytypic species, as are *Pan troglodytes* and *Gorilla gorilla* (Groves 1986), there appears to be no a priori reason to conclude that early hominids were not polytypic. This, however, does not preclude the possibility of different species within a genus (e.g., *Pan troglodytes* and *Pan paniscus*). Given the presumption of polytypism, it is most appropriate to compare a fossil hominid sample to as broad a range of modern referents as possible. The human data were not averaged in these populations to achieve one reference population, nor was the median population used as the sole reference population because it is important to visually represent the variability inherent in modern *Homo sapiens*.

The data on the buccal-lingual dimensions of the posterior teeth (P3 through M3) of the hominid fossil material from Swartkrans and Kromdaai were combined and analyzed to determine range, mean, standard deviation, and coefficient of variation. The results are listed in Table 1. Combined sample sizes for each tooth range from 18–31 with an average of 25, a size sufficiently large to provide strong confidence in the results of the CV analyses (Cope and Lacy, 1992). The CVs for each tooth of each reference population were obtained by utilizing the means and standard deviations of the buccal-lingual dimension for each maxillary and mandibular posterior tooth (see Table 2).

Analytic methods

The CVs of the combined Swartkrans/Kromdaai sample were then compared to the CVs of the reference samples. In addition, a computer simulation program (Cope and Lacy, 1992) which models the variability

TABLE 1. Coefficients of variation (CV) of posterior teeth (buccal-lingual breadth)[1]

	Swartkrans/Kromdraai combined					Swartkrans					Kromdraai				
	N	X[2]	SD	CV	Range	N	X[2]	SD	CV	Range	N	X[2]	SD	CV	Range
Maxilla															
P3	27	13.5	1.0	7.3	10.3–15.0	26	13.5	1.0	7.5	10.3–15.0	1	13.8	—	—	13.8–13.8
P4	31	14.8	1.0	6.7	12.8–16.3	30	14.8	1.0	6.8	12.8–16.3	1	15.3	—	—	15.3–15.3
M1	30	14.6	1.1	7.5	12.6–17.9	27	14.7	1.1	7.4	12.6–17.9	3	13.7	0.8	6.1	12.8–14.4
M2	26	15.9	0.9	5.5	14.3–17.5	25	15.9	0.9	5.6	14.3–17.5	1	15.8	—	—	15.8–15.8
M3	24	16.7	0.7	4.5	15.4–18.0	21	16.8	0.7	4.4	15.4–18.0	3	16.1	0.6	3.6	15.7–16.8
Mandible															
P3	18	11.8	0.9	7.7	9.4–12.9	15	11.7	1.0	8.2	9.4–12.9	3	11.9	0.6	5.1	11.3–12.5
P4	21	12.9	0.8	6.2	11.4–14.3	19	12.9	0.8	6.3	11.4–14.3	2	12.6	0.7	5.6	12.1–13.1
M1	28	13.7	1.0	7.5	11.8–15.8	25	13.9	1.0	6.9	12.0–15.8	3	12.5	0.7	5.2	11.8–13.1
M2	23	14.8	1.0	6.5	13.0–16.3	21	14.8	1.0	6.7	13.0–16.3	2	14.2	0.5	3.5	13.9–14.6
M3	23	14.6	1.0	7.0	12.8–16.5	21	14.6	1.1	7.3	12.8–16.5	2	14.4	0.5	3.4	14.0–14.7

[1] Data: Grine (1989); Wolpoff (personal communication).
[2] Mean buccal-lingual breadth in millimeters.

TABLE 2. Coefficients of variation (CV) of buccal-lingual tooth breadths of single taxon reference groups compared to the CVs of the combined Swartkrans/Kromdraai sample

Group	Mx P3	Mx P4	Mx M1	Mx M2	Mx M3	Mn P3	Mn P4	Mn M1	Mn M2	Mn M3	X/Pop[1]
Swartkrans/Kromdraii	7.3	6.7	7.5	5.5	4.5	7.7	6.2	7.5	6.5	7.0	25
Homo sapiens											
Thailand[3]	6.5	6.1	5.1	5.8	3.5	7.7	7.0	4.4	5.1	4.8	49
Thailand-Bronze Age[3]	6.5	5.5	4.4	5.5	12.6	7.6	7.0	4.7	5.1	5.8	45
China-Hong Kong[3]	5.5	6.5	4.9	7.2	11.5	7.5	6.9	5.4	6.4		31
China-Bronze Age[3]	5.4	5.9	5.0	5.5	8.9	6.2	5.8	4.6	5.2	7.2	247
Java[3]	5.8	5.5	6.0	7.5	12.6	10.8	5.1	5.6	6.9	8.3	33
Pecos Pueblo (800–1100)[3]	5.6	4.7	3.6	5.6	5.4	6.6	5.9	4.4	4.5	5.3	79
Tennessee Archaic[3]	10.4	5.3	5.0	5.9	7.2	6.1	6.0	4.5	8.4	6.5	40
Tennessee Woodland[3]	7.2	7.3	5.0	6.0	7.3	6.0	7.0	7.2	5.6	6.5	46
Tennessee Mississippian[3]	5.3	5.3	5.2	6.3	10.7	6.3	6.0	3.7	4.9	10.0	49
Hungarian Medieval[2]	6.8	7.2	4.9	7.7	8.9	7.0	7.3	5.0	6.0	7.4	185
Australian Aborigine[5]	6.1	5.9	5.2	6.3	8.6	6.8	6.7	5.0	5.4	6.6	209
Apes											
P. troglodytes[4]	7.0	6.1	6.3	9.1	10.8	10.8	7.2	6.4	7.2	9.5	243
G gorilla[4]	7.5	6.6	6.1	6.7	7.6	10.0	8.2	6.4	7.0	7.9	380
Extinct hominids:											
Afar/Laetoli[5]	5.5	6.5	7.3	5.5	11.6	10.3	7.2	6.2	7.8	6.5	12
Sterkfontein(M4)/Makapansgat[3]	6.0	6.5	6.2	6.9	8.2	8.5	5.9	7.8	8.8	7.5	18

[1] Average number of specimens per population.
[2] Data from Frayer (personal communication).
[3] Data from Kieser (1990).
[4] Data from Mahler (1973).
[5] Data from Wolpoff (personal communication).

found in living populations was used in the analysis.

The computer simulation procedure works as follows. A known single taxon reference group, which is presumed to share a phylogenetic relationship with the fossil group, is chosen. This group can be the reference population with the largest *n*. If the reference groups contain relatively few specimens, then the median CV from the reference groups for each tooth is used to create a median reference population. The mean buccal-lingual dimension and the standard deviation of each of the five maxillary and five mandibular posterior teeth of the appropriate reference population are used to generate the variability of the simulated population using the Monte Carlo method. (Although in their publication Cope and Lacy (1992) generated a population size of 10,000, the Turbo-Pascal Macintosh version of the program provided by Cope for this analysis was only capable of generating a population of 8,000 due to computation limitations.)

Once a population has been generated,

samples of a specified size are drawn without replacement from the population. The number of samples drawn equals the population size (i.e., 10,000 samples drawn from a population of 10,000; 8,000 samples from a population of 8,000). (However, in other versions of the program this is not necessarily the case [Cope, personal, communication].) The size of each sample to be drawn equates to the fossil sample size for that tooth.

The following example will clarify the procedure. For maxillary P3, a reference group has a mean buccal-lingual dimension of 9.64 mm with a standard deviation of 0.92. From this, a simulated, normally distributed population of size 8,000 with the same mean and standard deviation is generated. The fossil sample to be compared with the reference group contains 23 maxillary P3s; therefore, 8,000 samples of size 23 are drawn without replacement from the simulated population. CVs are calculated for each sample, resulting in a percentile sampling distribution of CVs based on the same sample size as the fossil assemblage in question.

The sampling distribution of CVs is listed in the form of percentiles where the ninety-fifth percentile point may be considered the critical value (alpha = .05). This is a one-tailed (directional) test. The alternate to the null hypothesis of a single species is that multiple species are being sampled since the posterior teeth have low variability and little sexual dimorphism (Cope, 1989; Cope and Lacy, 1992; Gingerich and Schoeninger, 1979). If the CV of the fossil sample exceeds the ninety-fifth percentile critical value, the null hypothesis is rejected.

Cope and Lacy (1992) analyzed this simulation approach to determine its ability to minimize type I error rates (rejecting a sample that is a single species) while maximizing power (rejecting a sample that is not a single species). Using four possible "fossil" sample sizes (n = 5, 10, 15, 20), they concluded that the reference group with the largest *n* (sample size) was better at minimizing type I errors but that the median reference group maximized power (while the type I error rate was higher than that for the largest *n* group, it did not significantly exceed 0.05). Given that an appropriate reference group has been selected, if the CVs for the posterior teeth of the fossil sample are consistently higher than the ninety-fifth percentile point of the simulated population, then the null hypothesis of sampling from a single taxon can be rejected (Cope and Lacy, 1992).

To develop a median reference population from the 11 modern human groups, the median CV for each tooth was determined, and the mean and standard deviation of the particular group from which the CV for that tooth came were used to generate a simulated reference population. For instance, the median CV for the maxillary P3 is 6.1, which is from the Australian aborigine group. Therefore, the mean and standard deviation from that group would be used to generate a simulated reference population for the maxillary P3.

The Australian aborigine groups has the second largest *n* of the human reference groups (209) but is more temporally restricted than the group with the largest *n* (China-Bronze Age = 247). Therefore, the Australian aborigine group was deemed appropriate for the largest *n* population simulation.

Of the remaining reference populations (*G. gorilla*, *P. troglodytes*, and fossil hominids), the *Pan* data was used to simulate a reference population because it has a large *n* and because *Pan* has a close phylogenetic relationship with modern humans (Caccone and Powell, 1989; Sibley and Ahlquist, 1984, 1987; Sibley, et al., 1990) and with fossil hominids.

Simulations were run each of the five maxillary and five mandibular teeth for each reference group. The ninety-fifth percentile critical values were obtained for the median reference population, the Australian Aborigines, the *Pan* (see Table 3).

The specific null hypothesis to be tested states that the CVs of the combined Swartkrans/Kromdraai sample are sampled from a single species population. The alternative hypothesis then states that if the combined Swartkrans/Kromdraai sample CVs exceed the reference CVs, then more than one species is present. Although this article deals specifically with whether there is sufficient reason to place the material from Swartkrans and Kromdaai into distinct species, CV analysis of hominid material from

TABLE 3. Ninety-fifth percentile critical value coefficients of variation (CV) of buccal-lingual tooth breadth in single taxon groups compared to the CVs of the combined Swartkrans/Kromdraai sample

Group	Mx P3	Mx P4	Mx M1	Mx M2	Mx M3	Mn P3	Mn P4	Mn M1	Mn M2	Mn M3	X/Pop[1]
Swartkrans/Kromdraai (not critical values)	7.3	6.7	7.5	5.5	4.5	7.7	6.2	7.5	6.5	7.0	25
Median reference group (based on all 11 human populations)[2]	7.4	7.1	6.1	7.4	11.0	8.8	8.8	5.8	6.6	8.1	Varies by tooth
Australian aborigines[3]	7.4	7.1	6.3	7.7	10.7	8.8	8.4	6.2	6.6	8.1	209
Pan troglodytes[4]	8.5	7.4	7.7	11.2	13.3	13.8	9.0	7.8	9.0	11.8	243

[1] Average number of specimens per population.
[2] Data from Frayer (personal communication), Kieser (1990), and Wolpoff (personal communication).
[3] Data from Wolpoff (personal communication).
[4] Data from Mahler (1973).

several other African sites (Omo, Turkana, and various permutations of the South African sites) was also done.

RESULTS

A comparison of the CVs for the combined Swartkrans/Kromdaai sample with the CVs for the Swartkrans sample alone (Table 1) shows that in every case, except for maxillary and mandibular M1 and maxillary M3, the Swartkrans material alone exceeds the combined sample CVs. In the case of the maxillary M1 and M3, the combined sample CVs are only 0.1 higher than the Swartkrans CVs for those teeth.

The buccal-lingual dimensions of the Kromdraai sample (Table 1) fall within the range of the Swartkrans sample, except for mandibular M1. One of the Kromdraai mandibular M1s has a breadth of 11.8 mm, while the smallest Swartkrans mandibular M1 measures 12.0 mm, a difference of only 0.2 mm. The narrow range of variability in the Kromdraai sample is evident in a comparison of the Kromdraai CVs with those of Swartkrans. In most cases, the addition of the Kromdraai material to that of Swartkrans reduces the relevant CV.

A tooth-by-tooth comparison of the Swartkrans/Kromdraai combined sample CVs with the CVs of the 11 modern human samples (see Table 2) shows that in every case, except for mandibular and maxillary M1, the combined Swartkrans/Kromdraai CVs fall within the range of variability of the modern human populations, which is clearly highlighted by Figures 1 and 2.

A comparison of the *Gorilla* CVs with those of the combined Swartkrans/Kromdraai sample shows that the reference sample CVs exceed those of the Swartkrans/Kromdraai sample except for maxillary and mandibular M1 and for maxillary P4 (where the difference is only 0.1). The results are similar when the Swartkrans/Kromdraai CVs are compared to *Pan*, although the CVs for both the Swartkrans/Kromdraai maxillary P3 and P4 exceed the CVs for those teeth in *Pan*. Again, the combined Swartkrans/Kromdraai CVs, as seen in Figures 1 and 2, fall within the range of these single taxon referents.

The comparison of the CVs of the single taxon fossil hominids from Afar/Laetoli and Sterkfontein/Makapansgat with the CVs of the combined Swartkrans/Kromdraai sample (see Table 2) results in conclusions in accord with those achieved by the comparison between *Pan* and Swartkrans/Kromdraai, as is highlighted in Figures 1 and 2.

In those cases where the Swartkrans/Kromdraai CVs exceed the CVs for the single taxon reference groups (modern humans, *Pan, Gorilla*, Afar/Laetoli, and Sterkfontein/Makapansgat), the CVs for Swartkrans alone also exceed those of these reference groups. The only exception is the CV for the Swartkrans mandibular M1, which falls below the relevant CV for two reference populations, Tennessee Woodland and Sterkfontein/Makapansgat. Given that the CVs for the Swartkrans sample are generally higher than the CVs for the combined Swartkrans/Kromdraai sample and given that the Swartkrans australopithecine material is accepted as representing a single species (Grine, 1988), there is no evidence that the

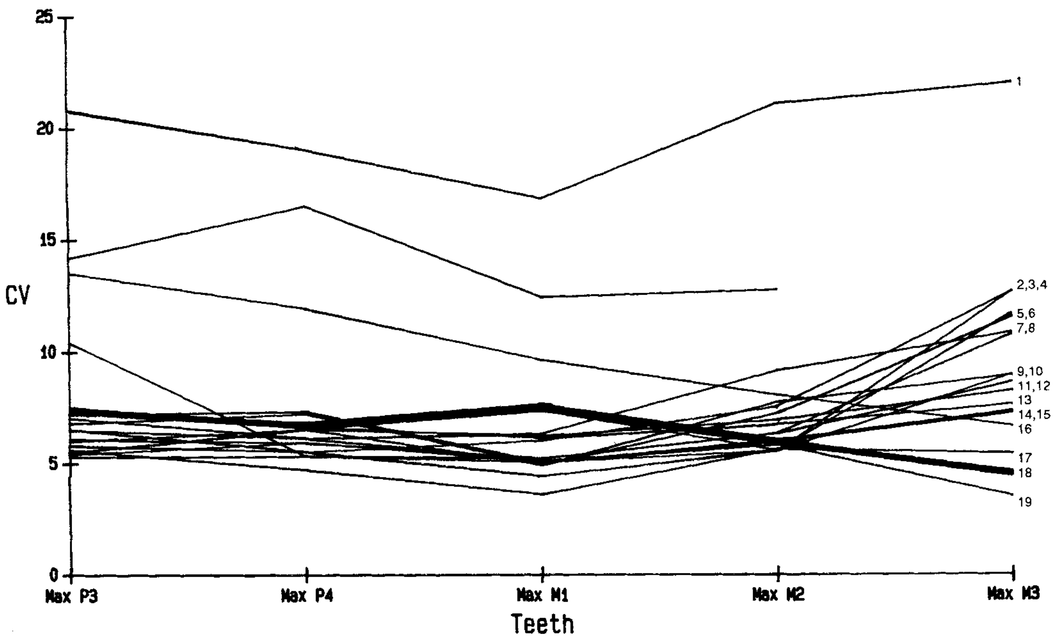

Fig. 1. Combined Swartkrans/Kromdraai coefficients of variation (CVs) of buccal-lingual tooth breadths compared to CVs of single taxon reference groups: maxillary dentition. 1, *G. gorilla*/*P. troglodytes;* 2, Turkana; 3, Java; 4, Thailand-Bronze Age; 5, Tennessee Mississippian; 6, China-Hong Kong; 7, *P. troglodytes;* 8, Afar/Laetoli; 9, Hungarian Medieval; 10, China-Bronze Age; 11, Australian aborigine; 12, Sterkfontein/Makapansgat; 13, *G. gorilla;* 14, Tennessee Woodland; 15, Tennessee Archaic; 16, Omo; 17, Pecos; 18, Swartkrans/Kromdraai; 19, Thailand. Items 2–6, 9–11, and 14, 15, 17, and 19 are *H. sapiens.*

Swartkrans/Kromdraai data contain multiple taxa.

On the other hand, analysis of the material from Omo and Turkana clearly indicates the presence of multiple species at each of these sites. (Compare Table 4 with the reference populations in Table 2.) Interestingly, the various permutations of the South African sites (Sterkfontein/Makapansgat/Kromdraai, Sterkfontein/Makapansgat/Swartkrans, and Sterkfontein/Makapansgat/Swartkrans/Kromdraai) do not indicate the presence of multiple species at these sites (see Table 4).

The ninety-fifth percentile critical value CVs of the median reference population and the Australian aborigines exceed the CVs of the combined Swartkrans/Kromdraai sample in all cases, except for the maxillary and mandibular M1s. The critical value CVs for *Pan* exceed the CVs for every tooth in the combined Swartkrans/Kromdraai sample including the maxillary and mandibular M1s (see Table 3). These results are consistent with the sampling of a single taxon at Swartkrans/Kromdraai.

Analysis of the various permutations of the South African sites were also done using the simulation technique (see Table 5). In eight out of ten cases, the Sterkfontein/Makapansgat and Kromdraai combined sample CVs are below the ninety-fifth percentile critical values. This is also true of the CVs of the Sterkfontein/Makapansgat sample. The two samples exceed the ninety-fifth percentile critical values for mandibular M2 and M3. In five out of ten cases, the Sterkfontein/Makapansgat and Swartkrans combined sample CVs are below the ninety-fifth percentile critical values. In 63% of the cases in which the Sterkfontein/Makapansgat sample CVs are below the ninety-fifth percentile critical values, the Sterkfontein/Makapansgat and Swartkrans combined sample CVs are also below the ninety-fifth percentile critical values. The maxillary M2,

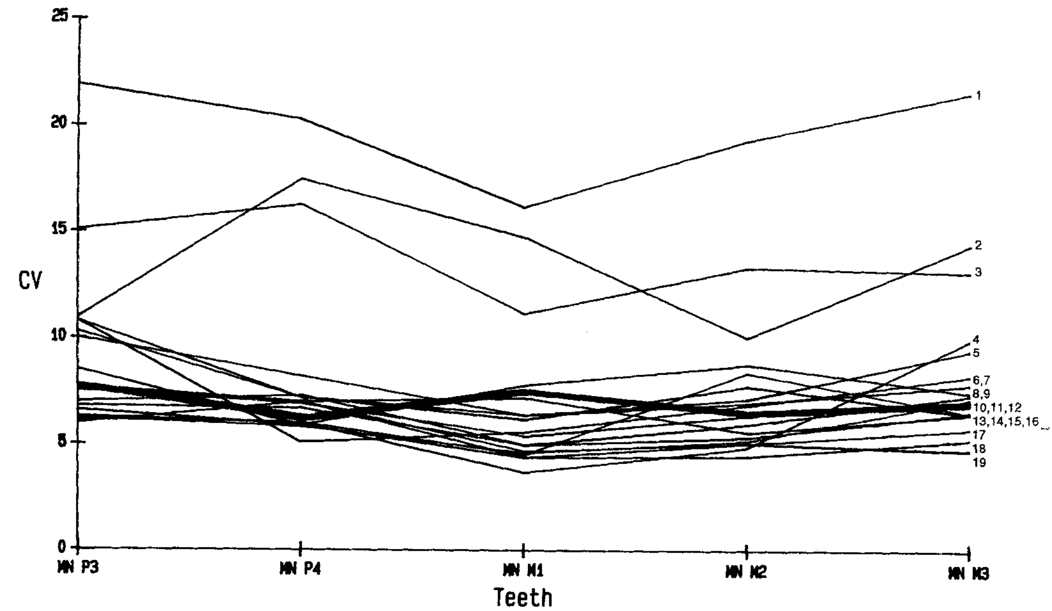

Fig. 2. Combined Swartkrans/Kromdraai coefficients of variation (CVs) of buccal-lingual tooth breadths compared to CVs of single taxon reference groups: mandibular dentition. 1, *G. gorilla / P. troglodytes;* 2, Omo; 3, Turkana; 4, Tennessee Mississippian; 5, *P. troglodytes;* 6, Java; 7, *G. gorilla;* 8, Sterkfontein/Makapansgat; 9, Hungarian Medieval; 10, China-Hong Kong; 11, Swartkrans/Kromdraai; 12, China-Bronze Age; 13, Tennessee Archaic; 14, Afar/Laetoli; 15, Tennessee Woodland; 16, Australian aborigine; 17, Thailand-Bronze Age; 18, Pecos; 19, Thailand. Items 4, 6, 9, 10, and 12–19 are *H. sapiens.*

TABLE 4. Coefficients of variation(CV) of buccal-lingual tooth breath of Omo, Turkana, and Gorilla / Pan (multiple species samples) and various permutations of the South African hominid samples[1]

Group	Mx P3	Mx P4	Mx M1	Mx M2	Mx M3	Mn P3	Mn P4	Mn M1	Mn M2	Mn M3	X/Pop[2]
Omo[3]	13.5	11.9	9.6	8.0	6.6	11.0	17.5	14.8	10.1	14.5	11
Turkana[3]	14.2	16.5	12.4	12.7		15.1	16.3	11.2	13.4	13.2	11
G. gorilla / P. troglodytes	20.8	19.0	16.8	21.0	21.9	21.9	20.3	16.2	19.4	21.7	670
Sterk[4]/Makapansgat	5.88	6.46	6.04	6.74	8.38	8.49	5.91	7.82	8.77	7.45	18
Sterk/Makapansgat/Kromdraai	5.97	7.07	5.96	6.61	8.16	7.77	6.15	7.78	8.48	7.00	20
Sterk/Makapansgat/Swartkrans	7.45	8.43	6.40	6.33	7.50	8.26	7.50	7.95	8.12	7.26	42
Sterk/Maka[5]/Swart[6]/Kromdraai	7.41	8.40	6.38	6.27	7.59	7.93	7.32	8.06	7.99	7.09	44

[1] CVs of combined data sets, as shown. For discussion, see text.
[2] Average number of specimens per population.
[3] Wolpoff (personal communication).
[4] Sterk = Sterkfontein.
[5] Maka = Makapansgat.
[6] Swart = Swartkrans.

whose CV for the Sterkfontein/Makapansgat and Swartkrans combined sample falls below the ninety-fifth percentile critical value, is considered one of the best teeth for determining the number of species in a sample (Gingerich and Schoeninger, 1979). (Both the Sterkfontein/Makapansgat sample CVs and Sterkfontein/Makapansgat and Swartkrans combined sample CVs exceed the critical value for mandibular M2.)

In summary, a comparison of the CVs of the combined Swartkrans/Kromdraai sample with the CVs of known single taxon samples clearly positions the combined Swartkrans/Kromdraai sample within the single taxon range. Further, the results of

TABLE 5. Coefficients of variation (CV) of buccal-lingual-tooth breadths of various permutations of the South African samples compared to the critical value CVs[1]

Group	Mx P3	Mx P4	Mx M1	Mx M2	Mx M3	Mn P3	Mn P4	Mn M1	Mn M2	Mn M3	X/Pop[2]
Sterk[3]/Makapansgat	5.88	6.46	6.04	6.74	8.38	8.49	5.91	7.82	8.77	7.45	18
Median referent	7.59	7.37	6.13	7.41	11.20	9.15	9.69	6.18	6.50	8.59	
Large *n* referent	7.54	7.41	6.35	8.42	10.82	9.14	9.18	6.60	6.83	8.67	
Sterk/Makapansgat/Kromdraai	5.97	7.07	5.96	6.61	8.16	7.77	6.15	7.78	8.48	7.00	20
Median referent	7.50	7.34	6.10	7.44	11.07	9.00	9.44	6.01	6.71	8.47	
Large *n* referent	7.54	7.35	6.34	8.39	10.71	8.85	8.94	6.48	6.74	8.48	
Sterk/Makapansgat/Swartkrans	7.45	8.43	6.40	6.33	7.50	8.26	7.50	7.95	8.12	7.26	42
Median referent	7.07	6.80	5.76	7.00	10.42	8.40	8.62	5.58	6.32	7.84	
Large *n* referent	7.08	6.83	5.99	7.97	10.07	8.44	8.16	5.97	6.32	7.84	
Sterk/Maka[4]/Swart[5]/Kromdraai	7.41	8.40	6.38	6.27	7.59	7.93	7.32	8.06	7.99	7.09	44
Median referent	7.06	6.82	5.75	7.00	10.39	8.37	8.55	5.53	6.28	7.81	
Large *n* referent	7.05	6.81	5.98	7.94	10.06	8.28	8.12	5.92	6.29	7.85	

[1] Median referent: based on 11 modern populations; large 'n' referent: Australian Aborigines. See text for discussion.
[2] Average number of specimens per population.
[3] Sterk = Sterkfontein.
[4] Maka = Makapansgat.
[5] Swart = Swartkrans.

the simulation analysis support this conclusion. Therefore, this analysis does not support the division of Swartkrans and Kromdraai into separate taxa.

DISCUSSION

While the CVs for the maxillary and mandibular M1s of the Swartkrans/Kromdraai combined sample fall below the critical value CVs for *Pan*, they exceed these values for the human reference groups. These teeth are, on average, much less variable in modern human populations than are the other posterior teeth. This would, naturally, lower the relevant CVs. The reason(s) for this lowered variability compared to the fossil sample is unclear. Geographic variation, which can result in high CVs for widely dispersed species (Plavcan, 1993), seem unlikely since the two sites are less than 3 miles apart (Brain 1958). Temporal variation may be a causative factor. While the australopithecine material from Swartkrans has been dated (Grine, 1988), that from Kromdraai has not been dated (the faunal material is not in association with the hominid material) and may be much older (Grine, 1988) or of approximately the same age as that of Swartkrans (Delson, 1988). Therefore, it is possible that the increased variability of the M1 is due to intraspecific variation (Plavcan, 1993).

The relative size of M1 in relation to M2 and M3 has altered from the period of the Swartkrans/Kromdraai sample to the present. In the Swartkrans/Kromdraai material the relationships among the molars were different, with M2 being larger than M1 and M3 larger than M2. In modern populations, the buccal-lingual dimensions of maxillary M1 and M2 are similar, while both are larger than M3. In mandibular molars, the buccal-lingual dimensions of all three teeth are fairly close, especially M2 and M3, while M1 is usually slightly larger.

It is possible that certain isolated teeth lacking roots which have been identified as M1s are in actuality dm2s or M2s. Different researchers working with the same material have come to different conclusions on which specimen belongs in which tooth category. The quantity of specimens per tooth for the Swartkrans australopithecine material differ by researcher (Grine, 1988; White et al., 1981; Wolpoff, personal, communication). In addition, certain teeth in the Omo australopithecine material which have been identified as mandibular M1s or M2s by one set of researchers (Howell and Coppens, 1974) have been identified as mandibular dm2s or M1s by another researcher (Wolpoff, personal communication). Therefore, the variable attribution of some teeth may be a causative factor in the higher CVs of M1/1.

To summarize, it is possible that the variable attribution of some teeth has resulted in elevated M1/1 CVs. On the other hand, the temporal span may be such that the

higher CVs could be due to intraspecific variation.

Intraspecific variation may also explain the results obtained from the analysis of the various permutations of the South African sites. While the addition of Kromdraai to Sterkfontein/Makapansgat sample could be viewed as signifying a single species, the addition of Swartkrans to Sterkfontein/Makapansgat sample could also be viewed as signifying a single species or, at the least, as very ambiguous, especially since the maxillary M2 for the combined sample of Sterkfontein/Makapansgat and Swartkrans falls below the ninety-fifth percentile critical value for that tooth. (The Sterkfontein/Makapansgat/Swartkrans/Kromdraai combined sample is similar to the Sterkfontein/Makapansgat/Swartkrans combined sample.) Sterkfontein/Makapansgat is generally accepted as representing a single species, while Swartkrans is accepted as representing a different species. In fact, some researchers (e.g., Grine, 1988) also view these species as representatives of distinct genera (*Australopithecus* and *Paranthropus*, respectively). However, combining the data of two modern hominoids usually accepted as representing distinct genera (*Gorilla* and *Pan*) results in extremely elevated CVs which greatly exceed the ninety-fifth percentile critical values (see Table 4).

As noted above, the method of analysis reported here effectively separates the known genera of *Pan* and *Gorilla*. Failure to separate the presumed genera of *Australopithecus* and *Paranthropus* leads to the following conclusions: 1) either the extensive time period which separates the samples is such as to confound the analysis, and so ambiguous results are to be expected, or 2) all the South African australopithecines are representatives of not only a single genus but a single species, and any resulting metric and morphological differences are simply the result of the extremely long time span over which the species evolved. Lack of generic distinctions among the South African hominids has also been noted by Dart (1948) and Wolpoff (1971b, 1980), who analyzed both the metrical and morphological data. As Tobias (1985) has observed regarding species and generic distinctions, there is a tendency to extrapolate broad phylogenetic conclusions from limited data.

As part of his phylogenetic system, Ax (1987) developed the evolutionary species concept which encompasses the dimensions of both time and space and which is defined as a lineage: the chain of ancestor-descendant populations which are reproductively connected to each other and at the same time distinct from other such lineages. As long as this reproductive connection is maintained, there could be an infinitely large number of genotypic changes with commensurate phenotypic diversity within the population, but there would still be only a single species, the same species it had been since it originated. Until segments of the population become reproductively isolated by unbreachable genetic barriers, there is no speciation. New material from Sterkfontein appears to support the lineage concept, as this material is described as "robust" and shows morphological overlap with material from Swartkrans (Wolpoff, personal, communication). Descriptions of this new material and further discoveries may lead to a clarification of any possible generic/species distinctions among the South African sites.

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